Impacts of extreme winter warming events on litter decomposition in a sub-Arctic heathland

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Abstract

Arctic climate change is expected to lead to a greater frequency of extreme winter warming events. During these events, temperatures rapidly increase to well above 0ºC for a number of days, which can lead to snow melt at the landscape scale, loss of insulating snow cover and warming of soils. However, upon return of cold ambient temperatures, soils can freeze deeper and may experience more freeze-thaw cycles due to the absence of a buffering snow layer. Such loss of snow cover and changes in soil temperatures may be critical for litter decomposition since a stable soil microclimate during winter (facilitated by snow cover) allows activity of soil organisms. Indeed, a substantial part of fresh litter decomposition may occur in winter. However, the impacts of extreme winter warming events on soil processes such as decomposition have never before been investigated. With this study we quantify the impacts of winter warming events on fresh litter decomposition using field simulations and lab studies.

Winter warming events were simulated in sub-Arctic heathland using infrared heating lamps and soil warming cables during March (typically the period of maximum snow depth) in three consecutive years of 2007, 2008, and 2009. During the winters of 2008 and 2009, simulations were also run in January (typically a period of shallow snow cover) on separate plots. The lab study included soil cores with and without fresh litter subjected to winter warming simulations in climate chambers.

Litter decomposition of common plant species was unaffected by winter warming events simulated either in the lab (litter of *Betula pubescens ssp. czerepanovii)*, or field (litter of *Vaccinium vitis-idaea,* and *B. pubescens ssp. czerepanovii*) with the exception of *Vaccinium myrtillus* (a common deciduous dwarf shrub) that showed less mass loss in

response to winter warming events. Soil CO_2 efflux measured in the lab study was (as expected) highly responsive to winter warming events but surprisingly fresh litter decomposition was not. Most fresh litter mass loss in the lab occurred during the first 3-4 weeks (simulating the period after litter fall).

In contrast to past understanding, this suggests that winter decomposition of fresh litter is almost non-existent and observations of substantial mass loss across the cold season seen here and in other studies may result from leaching in autumn, prior to the onset of "true" winter. Further, our findings surprisingly suggest that extreme winter warming events do not affect fresh litter decomposition.

Introduction

The Arctic is already experiencing warmer winter temperatures as a result of climate change and winter is predicted to continue to warm more than summer. Also predicted are increases in more extreme weather events (Shabbar et al. 2004; Liu et al. 2006; Christensen et al. 2007; Brown et al. 2008). Extreme winter warming events are already being observed in some Arctic regions, and these can result in complete snow melt across whole landscapes (Callaghan et al. 2004; Phoenix et al. 2004; Bokhorst et al. 2009). Vegetation and soils can than be warmed for short periods (e.g., 1 week) but afterwards are then exposed to the returning much colder winter temperatures and freeze-thaw cycles until a fresh layer of insulating snow is deposited. Such rapid temperature changes are likely to impact soil organisms and the processes they are involved in (e.g., decomposition) (Lipson et al. 2002; Mikan et al. 2002; Schmidt et al. 2004; Schimel et al. 2007) but this has never previously been investigated.

Extreme warming events are likely to increase microbial activity during winter, and may result in increased soil respiration and higher litter decomposition rates. This could increase the already substantial (~20% mass loss) litter breakdown over the cold season in Arctic ecosystems (Bleak 1970; Moore 1983, 1984; Taylor et al. 1990; Hobbie et al. 1996). Some studies suggest that microbial respiration of freshly-fallen litter subsequently covered by snow might even significantly contribute to total winter soil respiration (Uchida *et al.* 2005) which could -during a winter warming event- become even higher should microbial activity be stimulated. However, after such a warming event, soils no longer insulated by snow and may be subject to freeze-thaw cycles which

could cause an opposite ‘negative’ effect on microbial activity (Yergeau et al. 2008). The physical damage to litter in response to freeze-thaw cycles are generally believed to be short term and negligible compared to microbial activity in winter (Taylor et al. 1988).

In addition to uncertainty regarding the impacts of extreme warming events, there is also a more general question of when during the cold season most fresh litter decomposition occurs. Past studies have shown substantial cold season litter decomposition (Hobbie et al. 1996) but in such studies ‘cold season’ can be true winter only or include autumn and/or early spring. However, litter mass loss could happen during: a) litter leaching and active microbial breakdown in autumn, b) active microbial breakdown during winter (period with complete snow cover) and, c) active microbial breakdown and leaching as a result of spring snow melt. Further, impacts of winter warming events on fresh litter decomposition could make an important, yet currently unquantified, contribution to the annual ecosystem carbon budget of Arctic ecosystems but cannot be accurately predicted until it is clear when most microbial litter breakdown occurs during the cold season.

With these concerns in mind we determined the impacts of winter warming events on fresh litter decomposition using lab and field studies in sub-Arctic heathland – a common and widely distributed vegetation type. The field studies consisted of simulations of winter warming events on experimental plots using infrared lamps and soil warming cables with litter bags deployed to quantify fresh litter decomposition rates. We hypothesize that: 1) the winter warming events would temporarily increase decomposition due to higher microbial activity leading to larger litter mass loss rates, 2) generally more recalcitrant litter types (evergreen and bryophytes) are less likely to

104 respond to winter warming events than more easily decomposable litter types
105 (deciduous). This field work was supported by lab simulations of winter warming events
106 on soil cores with and without fresh litter. Soil cores were subjected to different number
107 and duration of winter warming events to determine the impacts of repeated and longer
108 events. We hypothesize here that 3) higher litter decomposition rates should be found in
109 longer winter warming events while more freeze-thaw events will reduce these rates. 4)
110 Microbial breakdown of fresh litter during winter warming events will increase total soil
111 respiration rates.
112

Materials and Methods

Simulation of extreme winter warming events

Simulations of winter warming events in the field were performed in a sub-Arctic heathland community close to the Abisko Scientific Research Station (ANS) in northern Sweden (68° 21' N, 18° 49' E). Full details of the research site and experimental set-up are described in Bokhorst *et al.* (2008). In brief, the experiment consisted of 24 plots, consisting of 6 control, 6 that were exposed to a week-long winter warming event in January using infrared heating lamps (800 W emitting at 3 μm; HS 2408, Kalglo Electronics Co., Bethlehem, USA), 6 for a similar winter warming event in March, and 6 plots that also ran in March which included heating lamps and additional soil warming to enhance soil thaw. Winter warming events were simulated in January (mid-winter) and March (late-winter) as the length of exposure to colder temperatures after such an event may affect winter litter decomposition.

Simulation of an extreme winter warming event started at the beginning of January and March for a period of seven days during which the lamps were kept at 50 cm distance from the snow surface and lowered accordingly as the snow depth decreased. This approach ensured gradual snow thaw, taking three days to thaw the full depth of snow in each plot (average starting snow depth, 50cm). As vegetation became exposed, lamps were kept at 70 cm above the soil surface, and we monitored leaf surface temperatures (Digitron 1408-K, Torquay, Devon, UK with type-K thermocouple) and canopy air and soil temperatures from the thermistors within the plots to ensure warming was realistic and within the bounds of temperatures recorded for real events. Soil

warming cables were switched on two days after the lamps to simulate the delay in soil thaw during a real event. Timing, rate and degree of warming were based on real events occurring in the Abisko region (Bokhorst et al. 2008). Heating lamps were removed from the frames at the end of the week-long warming treatment to avoid any shading effects of the lamps during the following growing season. Plots were then left untouched for the three remaining months of winter before data collection in spring and summer (June – August).

To monitor temperature changes, thermistors were placed in each plot at the soil surface, logging at 6-h intervals and recorded on a data logger (CR10 X Campbell Scientific, UK). Simulation of extreme winter warming events started at the beginning of January and March 2008 and 2009. The March plots had previously been exposed to a winter warming simulation in 2007 as part of a study of plant responses but decomposition studies were not undertaken then.

Litter decomposition in the field

Litter was collected during September 2007 by collecting senesced leaves shaken from abundant species: *Vaccinium myrtillus* (deciduous dwarf shrub), *V. vitis-idaea* (evergreen dwarf shrub) and *Betula pubescens ssp. czerepanovii* (deciduous tree). All samples were air-dried for 7d, after which they were placed in litter bags (6 cm × 6 cm with mesh size of 1.0 mm). Each plot received 16 litter bags, there being 4 each of *B. pubescens* (0.300 g dry weight equivalent of air dried material), *V. myrtillus* (0.150 g), and *V. vitis-idaea* (0.300 g). All weights were determined from air:oven dry (70ºC 48h) ratios determined from a subset of samples. Litter bags were placed in the plots on

September 22nd 2007 (just after the start of autumn in this region) and one litter bag of each type was retrieved in spring 2008 just after snow melt on May 10th to assess winter warming event impacts. Bags were also collected four weeks later on June 6th to determine the breakdown rates in early spring. Further collections were made in September 22nd 2008 and May 30th 2009 to assess the longer term impacts throughout summer and the effects of two years of winter warming events respectively. Litter mass-loss was measured after oven drying (70ºC 48h). C and N content of the litter was determined at the start of the experiment (by mass spectrometer, PDZ Europe 2020, SerCon, Crewe, UK).

Laboratory experiment of litter mass loss during winter with simulated extreme warming events

To quantify the impacts of winter warming events on fresh litter breakdown, a laboratory experiment was conducted with soil cores with and without surface fresh litter, and subjected to different winter warming events. Sixty-four soil cores (3.0 cm height with a diameter of 4.8cm) were collected from the dwarf shrub heathland around the field experiment during the autumn of 2007. Cores were placed in black PVC tubes with a closed mesh (0.5 mm) bottom and taken to Sheffield, UK. Vegetation and identifiable litter were removed from the top of the cores after which the cores were divided into four groups, of 16 cores each, which would receive different winter warming events. Cores were sealed at the bottom with cling film to prevent air exchange during respiration measurements, put into darkened plastic boxes, and placed in a climate chamber at 5 ºC.

To determine if fresh litter respiration substantially contributes to soil respiration (Uchida et al. 2005), 8 of the 16 cores of each group randomly received 0.400 g (corrected for oven-dried weight, 70ºC 48h) of air-dried senesced *B. pubescens* ssp. *czerapanovii* leaves (collected in autumn 2007 by shaking off the trees). This approximately equals the amount of litter that is commonly found on the top of the soil layer in the Abisko area per surface area (Rinnan *et al.* 2008). Total depth of the organic layer of the soil columns is less than found in the field which could lead to an overestimation of the contribution of fresh litter to soil respiration, none-the-less we chose to focus on the shallower soil depth since the upper layer will be first to thaw and be most responsive to a short natural warming event. Before placement, *Betula* litter was rewetted with a site-specific soil water extract (25ml) for two days to re-inoculate the litter with its microbial community. To enable build-up of the microbial community on the litter, the cores were kept at 5ºC for 30 days (starting mid October) before being transferred to a climate chamber kept at –5ºC.

Four different +5 ºC winter warming events were imposed on the soil cores: 2 types of "winter warming events" of 8-d total (a single 8 day event and a double 4 day event) and 2 of 16-d total duration (a single 16 days and 4 of 4 days). This design therefore allowed us to compare the impact of single vs. multiple events while holding the total degree days constant, and the impact of the total duration.

To reduce desiccation of litter and soil at sub-zero temperatures, cores were covered by a 2-cm thick layer of crushed ice in mesh netting (1 mm) which was removed before, and replaced after, respiration measurements. CO_2 production was measured by sealing the cores with a rubber septum, and taking a head space sample (2.0 ml) at 4 min

intervals. Air samples were immediately analyzed for CO_2 concentrations on an infrared gas analyzer (PP Systems EGM-1). CO_2 production was always measured the day before, and after a temperature change, and repeatedly between temperature changes until the end of April 2008 (day 184).

Litter was recovered from the cores after 184 days total incubation time, and was oven-dried at 70ºC for 48h, after which mass loss was determined. To estimate "autumn" mass loss in this laboratory study an additional five sets of litter samples (n=8) were rewetted and stored as described above. One set was immediately collected and oven-dried, another set was collected after 2-d followed by weekly sampling of the remaining three sets during the 30-d initial incubation period at +5ºC.

Statistical analyses

Differences in litter mass-loss between extreme winter warming events from the field were analysed with repeated measures ANOVA. Species difference in C and N content of litter was analyzed with a one-way ANOVA and post-hoc Tukey HSD. Repeated measures ANOVA was used to test for differences in respiration rate between soil cores with and without litter in the lab study. Differences in respiration rate between simulations of warming events in the lab were analyzed with repeated measures ANOVA for the -5 ºC measuring periods only. During warming simulations, respiration rates were compared between treatments using one-way ANOVA. Differences in litter mass-loss between simulations of warming events from the laboratory experiment were analyzed with one-way ANOVA. Homogeneity of variance was tested with Levene's test and log

transformations were applied where appropriate. All analyses were done in SPSS 14.0 (Chicago, Illinois, USA).

Results

Extreme winter warming events in the field

Soil surface temperatures increased during all winter warming events (Fig. 1). Following the warming simulations, soil surface temperatures fell to below these of the control plots and showed greater temperature fluctuations due to the absence of an insulating snow layer. However, this did not occur after the winter warming simulation of January 2008 as the end of the simulation coincided with a snowstorm burying the plots under new snow. Control plots remained between 0 and -5 °C during winter until the onset of spring.

Litter mass loss of *B. pubescens ssp. czerepanovii*, and *V. vitis-idaea* was unaffected by any of the winter warming events in the field (Fig. 2a,c). In contrast *V. myrtillus* had reduced mass loss (one-way ANOVA $F_{3,17} = 5.0$, $P < 0.05$) in all types of warming simulation plots in the spring following the 2nd winter of warming events (2009), by on average 24% compared to the controls (Fig 2b). Mass loss rates after the first winter were (from high to low): *V. myrtillus* (23.3 ±0.7%) > *B. pubescens ssp. czerepanovii* (19.0 ±0.8%) > *V. vitis-idaea* (16.7 ±0.4%) This pattern was consistent throughout the 20 months of litterbag incubation (Fig. 2).

Betula pubescens (62.4 ± 2.2) had the highest C/N ratio ($F_{2,15} = 21.9$, $P < 0.0001$) followed by, *V. vitis-idaea* (53.6 ± 0.8) and *V. myrtillus* (49.9 ± 0.7). The C/N ratio of *V. vitis-idaea* and *V. myrtillus* did not differ significantly (P = 0.13 Tukey HSD).

Litter decomposition and soil respiration during lab simulated warming events

Litter mass loss during the first 30 days at 5ºC was 17.6 ± 0.4% and did not differ significantly from mass loss at 184 days (Fig. 3) which was 20.0 ± 0.8, 20.6 ± 1.4, 20.1 ± 0.8 and 19.7 ± 0.9% for the 2 × 4 d, 1 × 8 d, 4 × 4 d and 1 × 16 d winter warming event simulations respectively. Litter mass loss of *B. pubescens* ssp. *czerapanovii* was similar for all types of winter warming event and appeared unaffected by duration or number of events ($F_{3,28} = 0.15$, $P = 0.93$).

Addition of fresh litter to soil cores did not affect total respiration rates in any of the winter warming simulations compared to the soil cores without litter (Fig. 4). Soil respiration during the laboratory experiment did respond strongly to temperature fluctuations with about 7 fold increase ($P < 0.05$ Tukey HSD) in respiration rate when the soil columns were placed at 5ºC. Soil respiration rates declined overall during the experiment but this decline did not differ between any of the winter warming simulation events (date: $F_{11,319} = 4.4$, $P < 0.00001$, date × treatment: $F_{11,319} = 0.95$, $P = 0.49$, treatment: $F_{1,29} = 0.94$, $P = 0.34$).

Discussion

Fresh litter decomposition during autumn, winter, and spring

The results from both our lab and field decomposition studies support the earlier findings of winter time litter decomposition experiments in that about 20% of fresh litter mass loss occurs in the cold season between litter fall and spring in high-latitude ecosystems (Bleak 1970; Abouguendia et al. 1979; Moore 1983, 1984; Hobbie et al. 1996). Indeed, our lab study showed strikingly similar amounts of mass loss as occurred in the field suggesting it was a good simulation for our decomposition study purposes. Further, our lab study also suggests that the majority (> 90%) of that mass loss occurs during the first weeks after litter fall and that very little (~2%) mass loss actually occurs during winter itself when temperatures are below 0°C (Fig. 3). These results suggest that the past observations of high winter litter mass loss (e.g., Hobbie et al. 1996) were not a result of active winter decomposition but instead of organic compounds leaching out prior to this in autumn. Active microbial breakdown of the fresh litter could have occurred before snow fall but no additional CO_2 efflux was detected during the first 4 weeks of the lab study. Microbial respiration of the fresh litter during this period should theoretically have doubled measured soil respiration rates from soil columns with fresh litter in comparison to those without. Therefore, it seems likely that autumn litter mass loss is mostly a result of organic compounds leaching out of the litter.

In the laboratory study, 61% of the observed “winter” mass loss occurred over the first two days of incubation in water: this further supports the hypothesis that autumn litter leaching is a major factor in “cold season” litter mass loss. This is comparable with findings from other litter leaching studies showing mass losses from 8 to 32% after 24

293 hours of leaching (Kučera 1959; Nykvist 1961; Gessner et al. 1989; Taylor et al. 1996;
294 Cleveland et al. 2004; Sasaki et al. 2007). A further 30% of the measured 'winter' litter
295 mass loss occurred during the 3-4 weeks of incubation at 5ºC in the lab. Therefore, in the
296 field even when assuming that litter on soil is not wetted as in the laboratory experiment,
297 a considerable mass loss through leaching could still occur between the 'autumn' period
298 after litter fall and before start of snow cover. We therefore propose that true 'winter'
299 decomposition of fresh litter is almost non-existent, and observations of cold season litter
300 mass loss are probably primarily driven by substantial mass loss in autumn.

301 The lack of response of fresh litter decomposition to winter warming events in the
302 field experiment can be explained from the findings that probably no breakdown actually
303 occurs during winter. In fact, *V. myrtillus* litter mass loss was actually reduced in the
304 winter warming plots (May 2009 analysis), contrary to our hypothesis. The reduced mass
305 loss could be a result of colder soil temperatures (due to lack of snow insulation)
306 following the warming events negatively impacting soil organisms (Sulkava et al. 2003)
307 resulting in reduced litter decomposition rates, but this would then have to be a lasting
308 effect into the following summer and autumn as no actual mass loss occurs during winter.
309 Another or additional possible cause could lie in increased *Empetrum hermaphroditum*
310 litter input resulting from damage to this species as observed in the winter warmed plots
311 (reported in Bokhorst et al. (2009)). Litter from this species contains considerable
312 amounts of phenolic compounds (Wallstedt *et al.* 2000) with allelopathic properties
313 inhibiting ecosystem processes such as nutrient cycling and decomposition (Wardle *et al.*
314 1998). That none of the other litter types were affected may perhaps be a result of
315 differences in litter chemistry and structure. *V. myrtillus* has fragile leaf litter and the

316 lowest C/N ratio making it the most easily degradable litter type and perhaps more
317 susceptible to changes than tougher litter types of *B. pubescens ssp. czerepanovii* and *V.*
318 *vitis-idaea*.

319 Litter breakdown rates followed general patterns in relation to leaf chemistry with
320 higher mass loss from litter with lower C/N ratios (Aerts 2006), though leaching or loss
321 of water soluble substances from the leaves could be an alternative mechanism behind the
322 observed differences between species in mass loss after winter (Taylor et al. 1996;
323 Gessner et al. 1999).

324 *B. pubescens ssp. czerepanovii* litter mass loss from the laboratory and field
325 experiments were comparable, both ± 20%. This is surprising as litterbags in the field
326 experienced spring snow melt (plus an extra melt in the winter warmed plots) which
327 could have leached considerable amounts of organic compounds while snow melt did not
328 occur in the lab study. Measurement of water soluble substances from the litter at these
329 potential crucial moments, in terms of litter mass loss, would have provided indications
330 of the leachability of chemical and structural litter compounds during these events
331 (Gessner et al. 1999). The data so far suggests that we may speculate that spring snow
332 melt may cause little leaching of fresh litter and does not contribute to fresh litter
333 decomposition. Further studies with a more frequent sampling rate than in this study, are
334 required to provide a definitive answer to the extent that spring snow melt plays in litter
335 decomposition.

336

337 *Old versus fresh litter*

Simulated extreme winter warming events (laboratory study) had an immediate and strong impact on soil respiration. Fresh litter however, remained mostly unaffected as seen with no additional mass loss in the field and lab or absence of measurable contribution to CO_2 flux in the lab. This is surprising as fresh litter generally has the most easily degradable organic compounds while older organic material in the soil (which would have contributed to the soil respiration seen) is more recalcitrant. These findings could suggest that this older material might be more responsive to an extreme winter warming event than fresh litter. Soil organisms regulate organic matter decomposition and different soil functional groups generally inhabit those different stages of litter, fresh and old (Berg et al. 1998; Hunter et al. 2003), suggesting that perhaps either some soil groups were absent from soil surface to participate in fresh litter decomposition (Heemsbergen et al. 2004) or that these were not activated during the winter warming event while those lower in the soil stratum were. Another reason for not observing additional responses from the fresh litter could be moisture limitation (Aerts 2006). During winter warming simulations in the field surface litter occasionally appeared dry and this could have reduced microbial activity. This drying could be a normal side effect of extreme winter warming events thereby not stimulating additional fresh litter mass loss. However, litter was constantly moist in the lab studies during warming event simulations suggesting that microbial activity on fresh litter is limited during winter warming events irrespective of moisture limitation. Furthermore, we cannot exclude the possibility that in exposed locations, litter decomposition could be facilitated by fragmentation by ice crystal blast during high winds. However, the dense dwarf shrub canopy in our experimental site (which is typical of large areas of dwarf shrub

vegetation) combined with few high winds during the warming means this was unlikely to occur.

Finally, it should also be acknowledged that more work would be needed to determine the broader applicability of our field simulation findings to other Arctic ecosystems. For instance, snow depth, slope and aspect will influence the extent of snow thaw and subsequent warming of the soil, while litter of other vegetation types may respond differently to those litters studied here, with responses being mediated further by local environmental conditions. None-the-less, dwarf shrub heathland is a widespread vegetation type with circumpolar distribution, and we can at least have confidence that these finding are therefore applicable to the large areas of the Arctic where this vegetation occurs.

Conclusion

Our lab study suggests that most cold season mass loss of fresh litter occurs in autumn before onset of winter and that fresh litter decomposition during the true winter period with snow cover is almost non-existent. Thus, earlier findings of large litter mass loss during the "cold season" may be incorrect (should our findings be broadly true for other Arctic ecosystem), unless autumn was considered to be part of this period. We hypothesized that during a winter warming event the microbial activity would increase, thereby affecting decomposition rates. Winter soil respiration rates in the lab were certainly increased but fresh litter decomposition was not. Both the repeated warming and freezing in the lab and the simulated winter warming events in the field had no effect on

383 total litter mass loss, indicating that freeze-thaw cycles caused by winter warming events
384 do not affect fresh litter decomposition.
385

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Figures

Figure 1. Soil surface temperatures during winters of 2008 and 2009. Extreme winter warming events raised soil temperatures during January and March (grey areas). Data points represent mean daily values from 6 plots for each treatment, error bars are SE. For clarity, only every other daily mean is shown. The warming event in January 2008 was followed by a snow storm thereby covering the exposed plots with a fresh layer of snow. Note that January and March plots are separate plots and experienced a warming event in January or March, not both.

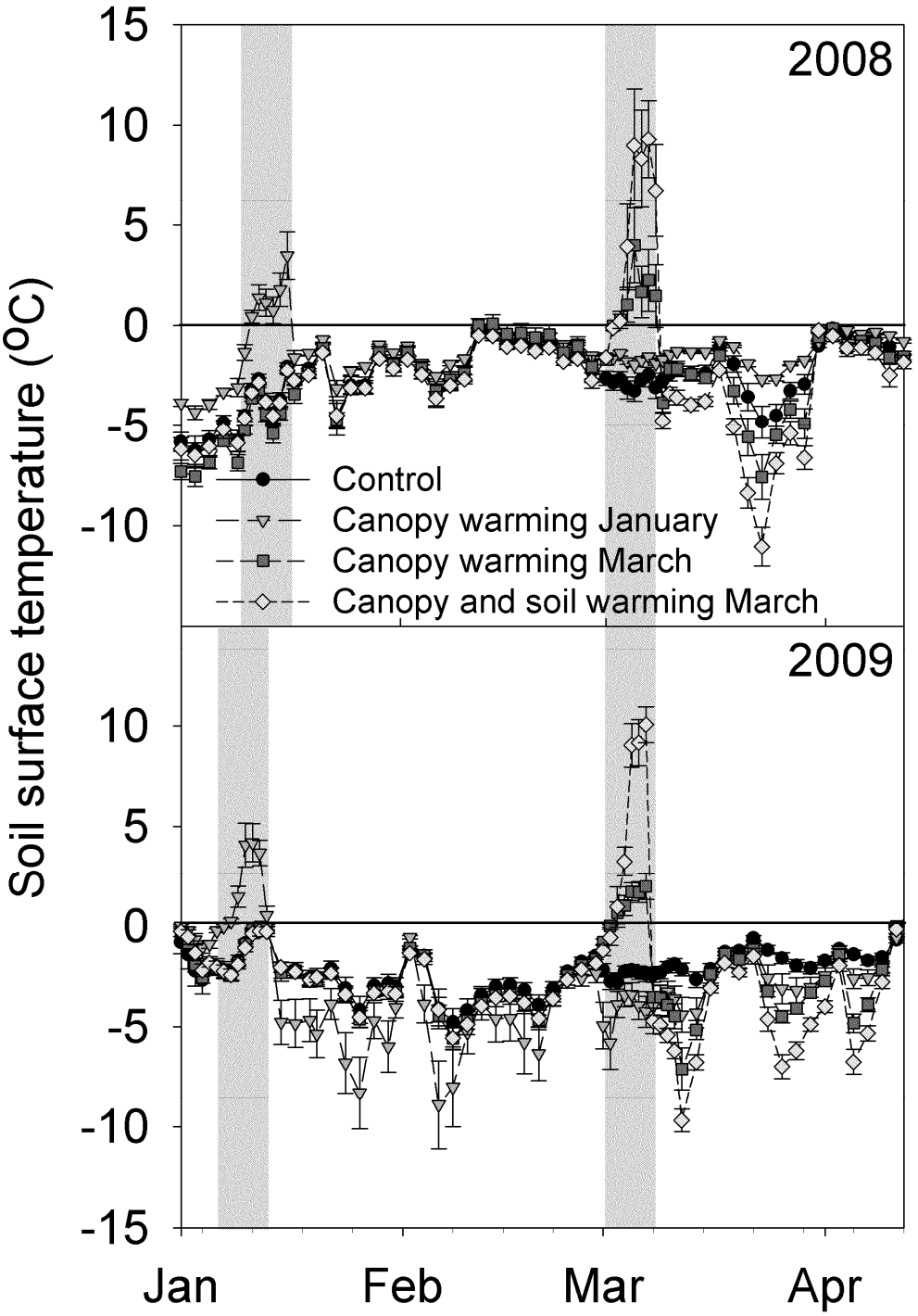
Figure 2. Litter mass loss after winter warming simulations in a sub-Arctic heathland. Litterbags with a) *Betula pubescens ssp. czerepanovii,* b) *Vaccinium myrtillus,* and c) *V. vitis-idaea* were retrieved after 8, 9, 12 and 20 months in the field following week-long winter-warming simulations during the first week of either January or March of 2007/8 and 2008/9. Winter-warming simulations did not affect litter decomposition rates, with the exception of *V. myrtillus* where mass loss in the control plots was higher than winter-warming treatment after 20 months (one-way ANOVA $F_{3,17}$ 5.0, $P < 0.05$, last sampling date only). Winter period is indicated by grey bars on graphs. Data points represent mean values from 5-6 plots for each treatment, error bars are SE. Note that the initial mass loss from September until May is unlikely to be linear (as suggested by Figure 3).

Figure 3. *Betula pubescens ssp. czerepanovii* litter mass remaining after 30 days incubation at 5ºC. Data points represent mean of 8 litter samples collected immediately after incubation in soil water extracts (day 2), followed by weekly sampling. Data point at

day 184 is from the litter samples (n=8) collected after incubation at -5ºC and winter-warming simulation (2 × 4 days data shown only as winter warming events had no impact on litter mass loss). Different letters indicate significant differences ($P < 0.05$ Tukey HSD) between mass loss over time, error bars are one SE but are generally smaller than the data-point size.

Figure 4. Winter soil respiration rates with warming simulations in the laboratory. Soil respiration from soil cores with (n=8) and without litter (n=8) kept at -5ºC from the 8th of November 2007 till 22nd of April 2008. The first three dates were taken while the cores were kept at 5ºC. Litter addition did not increase total respiration rates. a) 2 × 4 days (litter: $F_{1,13}$ 0.35, $P = 0.56$, date: $F_{18,234}$ 16.6, $P < 0.00001$, date × litter: $F_{18,234}$ 0.53, $P = 0.94$). b) 1 × 8 days (litter: $F_{1,14}$ 0.93, $P = 0.35$, date: $F_{16,224}$ 12.1, $P < 0.00001$, date × litter: $F_{16,224}$ 0.75, $P = 0.74$). c) 4 × 4 days (litter: $F_{1,14}$ 0.40, $P = 0.54$, date: $F_{22,308}$ 9.5, $P < 0.00001$, date × litter: $F_{22,308}$ 0.83, $P = 0.69$). d) 1 × 16 days (litter: $F_{1,13}$ 0.11, $P = 0.75$, date: $F_{17,221}$ 14.11, $P < 0.00001$, date × litter: $F_{17,221}$ 0.81, $P = 0.68$). Each point is the mean of 8 replicates, error bars are SE. * indicate significant differences ($P < 0.05$ Tukey HSD) in respiration rates between measuring dates just before, during and after winter warming events. Grey bars indicate the warming periods.

544 Figure 1



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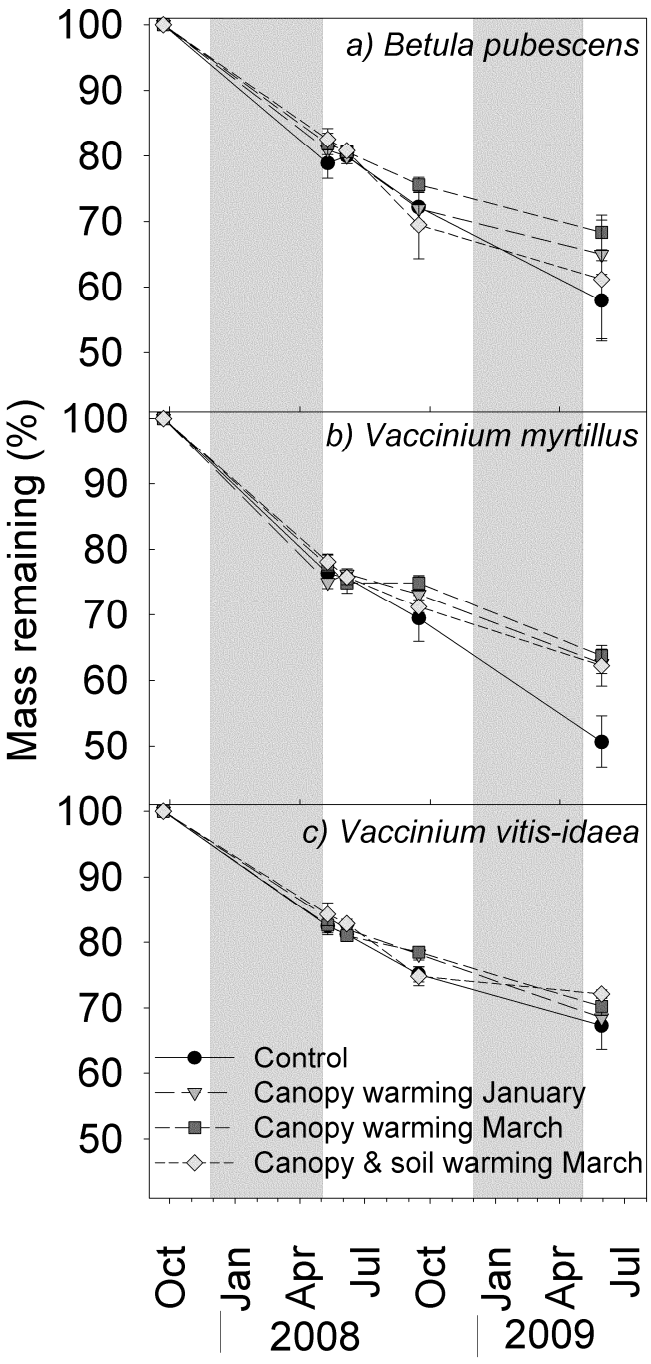
548 Figure 2



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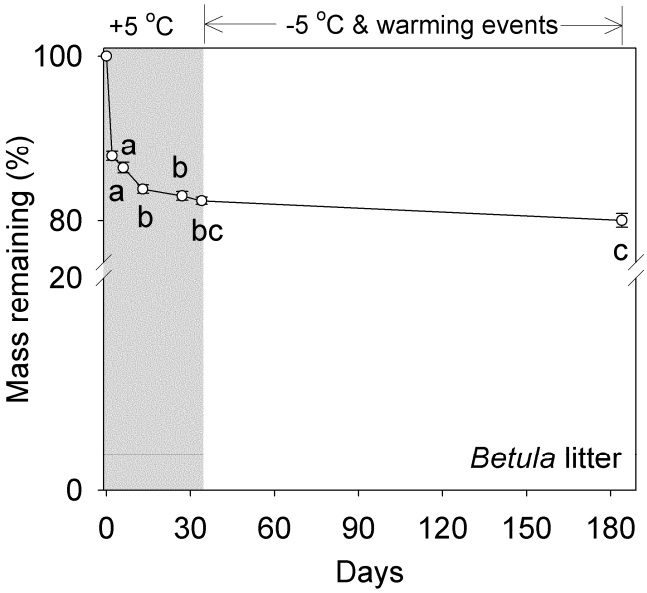
553 Figure 3



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558 Figure 4

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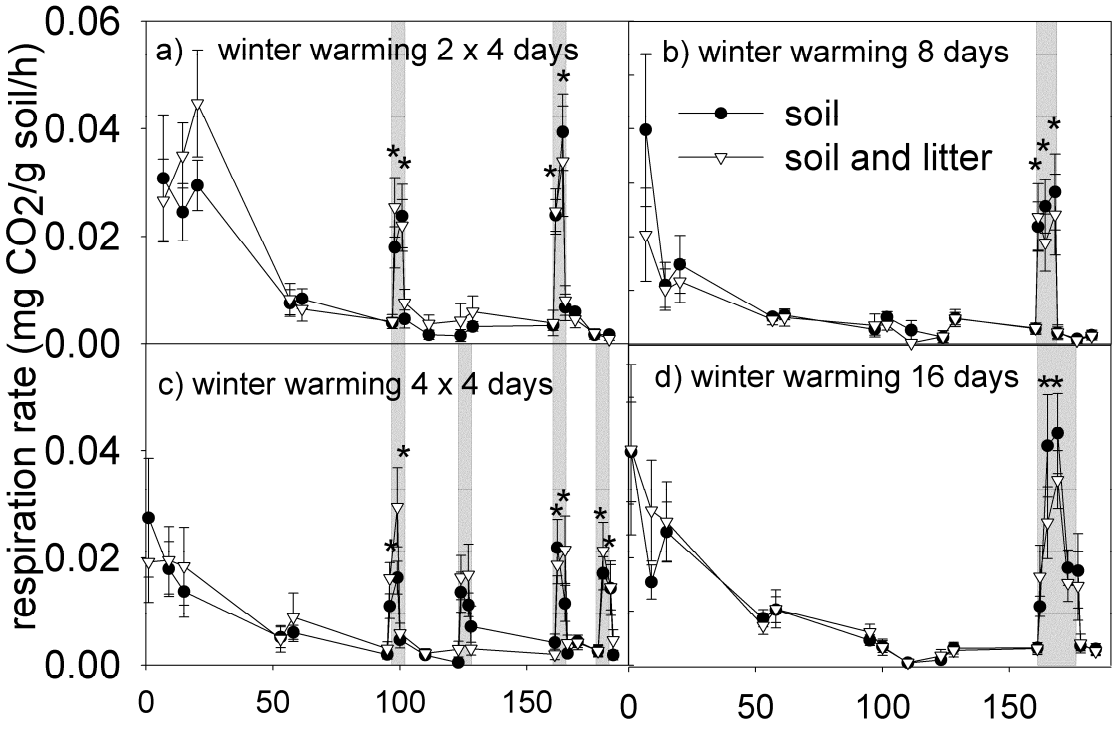

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